

GENITALIC CHARACTERIZATION, ENLARGEMENT, AND
REASSOCIATION OF THE NEOTROPICAL HESPERIINE
GENUS *HALOTUS* (HESPERIIDAE)

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ABSTRACT. Since classical characters involving facies, antennae, palpi, leg spines, wing shape, and venation do not, as previously used, rigorously delimit the genus *Halotus*, I do so using male genitalia. *Halotus* comprises three species: *H. angellus* (Plötz), the type, from at least Costa Rica and western Panama; *H. jonaveriorum* **new species** from Oaxaca, Mexico, which superficially looks like the type species; and *H. rica* (Bell) from southern Mexico to Costa Rica (and Ecuador?), which departs sharply from the other two species with respect to both facies and the male stigma. Mostly from male genitalia, I argue that *Halotus*, number 27 in Evans's (1955) 36-genus M or *Hesperia* group (the group most prevalent in the United States and Canada), relates to *Niconiades*, number 11 in his 20-genus O or *Calpodes* group. Evans's system of new world hesperiine generic groups is fatally flawed.

Additional key words: genitalia (male), stigma, taxonomy, generic groups, *Niconiades*.

I meant it when I wrote that "much of Evans's taxonomic system just below the level of the subfamily may be invalid" (Burns 1990:11). I was referring to his placement of 184 genera of American hesperiine skippers in 8 generic groups, lettered H to O (Evans 1955), and was extrapolating from the fact that *Amblyscirtes*, in his N or *Lerodea* group of 4 genera, belongs not with fellow groupies but with a few scattered genera in his 53-genus J or *Apauustus* group. Adding fuel to the fire, I argue here that genus *Halotus*, number 27 in Evans's 36-genus M or *Hesperia* group (the group most prevalent in the United States and Canada), relates to *Niconiades*, number 11 in his 20-genus O or *Calpodes* group.

Originally monotypic, *Halotus* is a small but growing genus that is strictly neotropical. Godman (1900:505) proposed it to accommodate a species (which he knew from two Costa Rican males) set off from external look-alikes by "the form of the brand [stigma]" and "the peculiar structure of the genitalia" (Fig. 1). Four decades later, Bell (1942) described a second species from a lone Costa Rican male, whose genitalia he figured but wrote nothing about. Because the upper side of its wings reminded Bell of *Atrytonopsis python* (Edwards), he put his new species in *Atrytonopsis*, whose genitalia differ greatly from those of *Halotus* (see Skinner & Williams 1924 [or Lindsey et al. 1931], Burns 1982, 1983). Evans (1955) correctly associated the two *Halotus* species, which differ substantially from each other in appearance. Now, half a century after Bell, I describe a third species from southern Mexico that super-

ficially looks like the first and genitally approximates the first in some respects, the second in others (while expressing its individuality).

I recharacterize the genus *Halotus* in terms of male genitalia (omitting female genitalia because females of two of the three species are lacking). The generic characters of Godman (1900) and Evans (1955) involve facies, antennae, palpi, leg spines, wing shape, and venation. As presented, these classical characters restrict the hesperiine field considerably but do not rigorously delimit *Halotus*.

Everyone wants to know about facies; but, because it can be so misleading, and because it has been so misread in the past, I play it down. In *Halotus*, as in so many other skippers, the ground color is dark brown, semihyaline spots variably relieve it in standard positions on the forewing (in spaces 2, 3, 6, 7, 8, and the cell), opaque spots sometimes mark the forewing (in space 1b) and dorsal hindwing (in spaces 2, 3, 4, 5, and the cell), and an elaborate system of opaque spots and overscaling creates a relatively complex ventral hindwing. (Bell [1942:4] thoroughly covers the ventral hindwing pattern in his description of *Halotus rica*.) What is far less common, the fringes of the wings are checkered in *Halotus* (see Figs. 14–19).

Judging from *H. rica* (the one species whose female I have seen), *Halotus* is not sexually dimorphic in color pattern. Although *Halotus* males do have a stigma on the dorsal forewing, its form is too inter-specifically variable (Figs. 11–13) to sharply define the genus.

In citing specimens, I place genitalic dissection numbers in brackets, museum abbreviations in parentheses. X-rated dissections are mine; the rest I credit individually. All dissected genitalia remain free in vials except those from the holotype of *Atrytonopsis rica* Bell, which are stuck on a slide. AMNH denotes the American Museum of Natural History, New York, N.Y.; USNM, the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Halotus Godman, 1900

(Figs. 1–10)

Type species. *Hesperia angellus* Plötz (1886:94) = *Hesperilla saxula* Mabille (1891: LXXXI) = *Halotus saxula* Godman (1900:505, pl. 95, figs. 42–44).

Male genitalia. Overall, the tegumen, uncus, and gnathos look oddly squat (Figs. 2, 5, 8). The uncus is slightly divided (Figs. 2, 5, 8) and shorter than the gnathos (Figs. 1, 2, 3, 5, 6, 8, 9).

The outer side of the valva is simple; the inner side, complex. In lateral view, at about the middle of the posterior margin, a small rough point points backward; below this point, it looks as though the posteroventral corner of the valva were bitten off (Figs. 1, 3, 6, 9). In dorsal or, better, ventral view, almost the distal third of the valva presents an inwardly produced and wickedly toothed flange. In the paired valvae, these dentate flanges suggest jaws that could have taken the posteroventral bite out of those valvae (Figs. 4, 7, 10)! Arising dorsal to the flange, toward the top of each valva, a more or less oblong, distally dentate projection extends anteromediad (Figs. 1, 3, 4, 6, 7, 9, 10).

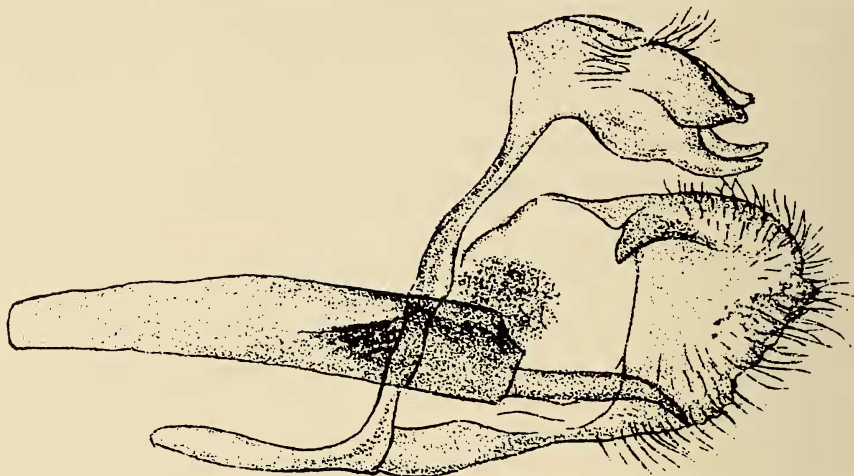


FIG. 1. Male genitalia of *Halotus angellus* from Irazú, Rio Sucio, COSTA RICA (ex Godman 1900:plate 95, fig. 44). Complete genitalia (minus left valva) in left lateral view. This figure presents the inner surface of the right valva whereas those that follow present the outer surface of the left valva.

The main body of the aedeagus, which is neither thick nor thin, is fairly uniform in diameter and fairly short—about three-fourths as long as the total intact genitalia (i.e., saccus plus valvae) (Figs. 1, 3, 4, 6, 7, 9, 10). The aedeagus ends ventrally in one or two robust, caudally directed, pointed prongs (Figs. 1, 3, 4, 6, 7, 9, 10). Its vesica carries three cornuti: a band of numerous spines, set in membrane, and two distinct, well-sclerotized units with one to several points (Figs. 3, 4, 6, 7, 9, 10). Myriad tiny spines crowd circumphallic membrane in a peculiar field just above the aedeagus (well above the juxta) (Figs. 3, 4, 6, 7, 9, 10).

The juxta lies ventral and lateral to the aedeagus, forming what amounts to an oblique U, but sits well back, quite hidden behind the valva, or valva plus vinculum, in lateral view (Figs. 3, 6, 9). Its transverse base has a concave anterior margin (Figs. 4, 7, 10), a pair of stubby, anteriorly- or anterolaterally-directed prongs at its anterolateral corners (Figs. 4, 7, 10), and a midventral, triangular projection (Figs. 4, 7, 10) that points anteroventrally (Figs. 3, 6, 9). On either side, two major lines of the U-shaped juxta cross in the narrowed zone where the ventral base connects with the broad, lateral arms (Figs. 3, 6, 9).

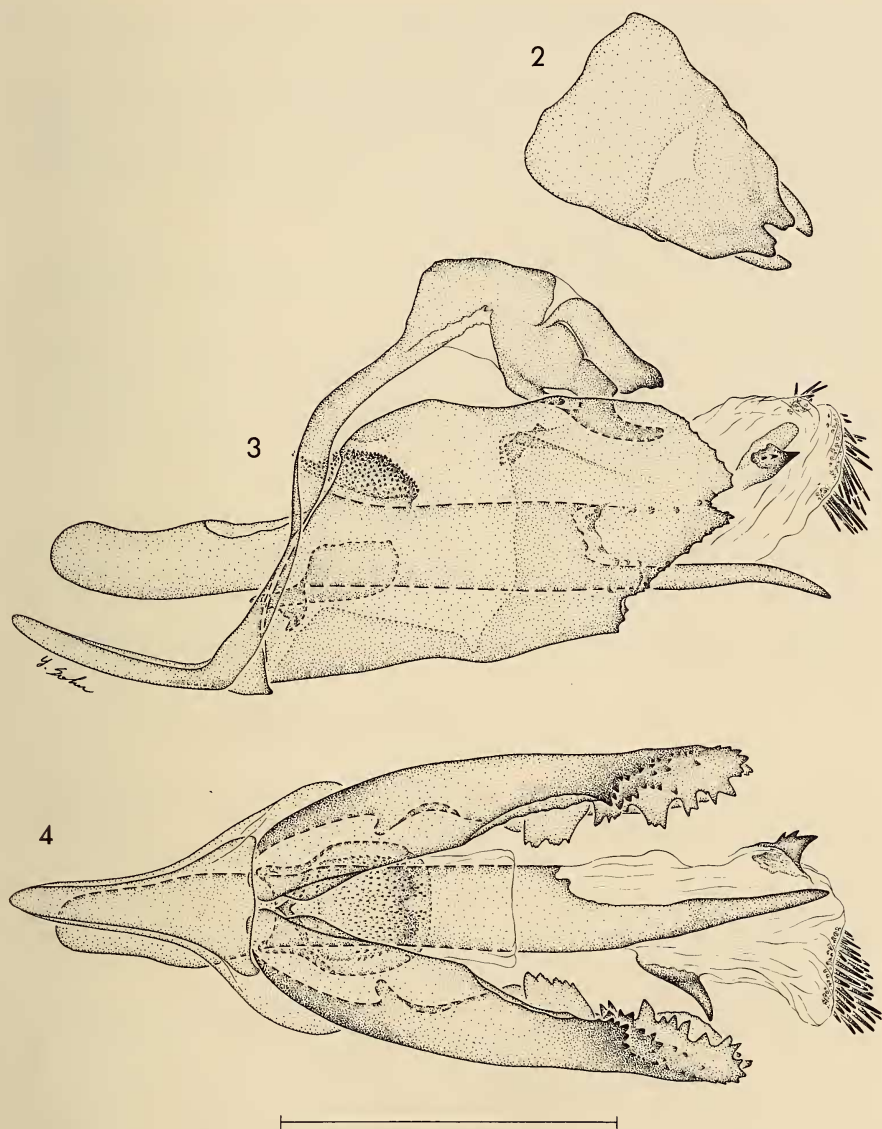
Geographic distribution. Middle elevations from southern Mexico (Jalisco, Puebla, Guerrero, Oaxaca, Chiapas) through Central America (Guatemala, El Salvador, Honduras, Costa Rica, western Panama [Chiriquí])—plus Ecuador (?).

Halotus angellus (Plötz)

(Figs. 1–4, 11, 14, 15)

Male genitalia (Figs. 1–4). Large gap between uncus and gnathos in lateral view (Figs. 1, 3). Each division of the divided uncus dual in dorsal view and slightly longer laterally than medially (Fig. 2).

In lateral view, rough point near middle of posterior margin of valva short and sharp (Figs. 1, 3). "Bite" out of ventrolateral corner of valva intermediate in depth and comparatively straight edged (Figs. 1, 3). Inwardly produced, wickedly dentate, "jawlike" flange set relatively high on valva—about midway between top and bottom of valva (Figs.



FIGS. 2-4. Male genitalia of *Halotus angellus* from Volcán Baru, 1800 m, Chiriquí, PANAMA, 5 December 1976, S. S. Nicolay [X-3089] (USNM). Scale = 1.0 mm. 2, Tegumen, uncus, and gnathos in dorsal view; 3, Complete genitalia (minus right valva) in left lateral view, with vesica everted (the simpler of the two discrete cornuti does not show at this angle); 4, Valvae, aedeagus (vesica everted to show cornuti), juxta, field of spines above aedeagus, saccus, and ventralmost vinculum in ventral view.

3, 4). Teeth on dorsal, oblong, anteromedially running projection of valva relatively coarse (Fig. 4).

One long prong at distal end of aedeagus on the right (Figs. 1, 3, 4). Cornutal spines larger and fewer (Figs. 3, 4) than in the other species of *Halotus*. The two discrete cornuti dissimilar: one a single, sharp, conspicuous point sprouting from one end of a low, elongate base (about like both of the discrete cornuti in *rica*); the other with multiple serrations sprouting from the middle of a low base (Figs. 3, 4). Field of numerous tiny spines above aedeagus at least as long as wide, and barely wider than aedeagus (Figs. 3, 4).

Midventral, triangular projection of juxta small (Figs. 3, 4).

Saccus the longest in the genus (Figs. 3, 4).

Stigma (Fig. 11). Inconspicuous. Bipartite: a triangular element in the angle between the cubitus and vein 2, not quite filling the apex of that angle; plus a linear element immediately below, along the lower side of vein 2.

Facies (Figs. 14, 15). Forewing cell and dorsal hindwing without spots. Semihyaline spots of forewing whitish or dirty white. That in space 2 usually shaped like > on the left and < on the right. Of the three small subapical spots in spaces 6, 7, and 8, only 7 always developed; and 6 more likely to dwindle than 8. Opaque spot in space 1b, just above vein 1, rudimentary to absent dorsally. Complex pattern of ventral hindwing mostly in shades of tan and brown and not contrasty.

Size (male forewing length). Mean 14.8 mm, range 14.0–15.4 mm, $n = 7$; the smallest species.

Type locality. Chiriquí.

Material examined. $n = 7$. COSTA RICA, Mount Poas, December, 2 ♂ [X-3088] (USNM).

PANAMA, CHIRIQUI: Volcán, 1465 m, 23 August 1964, 2 ♂, G. B. Small [H 304, S. S. Nicolay] (USNM); 30 June 1965, 1 ♂, G. B. Small (USNM). Volcán Baru, 1800 m, 5 December 1976, 2 ♂, S. S. Nicolay [X-3089] (USNM).

Steinhauser (1975) lists 15 ♂ of *H. angellus* from a single locality in western El Salvador. I do not know whether they belong to this species or the next.

Halotus jonaveriorum, new species

(Figs. 5–7, 12, 16, 17)

Male genitalia (Figs. 5–7). Large gap between uncus and gnathos in lateral view (Fig. 6), as in *angellus*. Each division of the divided uncus dual in dorsal view but slightly longer medially than laterally (Fig. 5)—and therefore visibly dual in lateral view, as well (Fig. 6).

In lateral view, rough point near middle of posterior margin of valva short and truncate (Fig. 6). "Bite" out of ventrolateral corner of valva comparatively deep and curved (Fig. 6). Inwardly produced, wickedly dentate, "jawlike" flange set relatively low on valva—closer to bottom than top of valva (Figs. 6, 7). Teeth on dorsal, oblong, anteromedially running projection of valva relatively fine (Fig. 7).

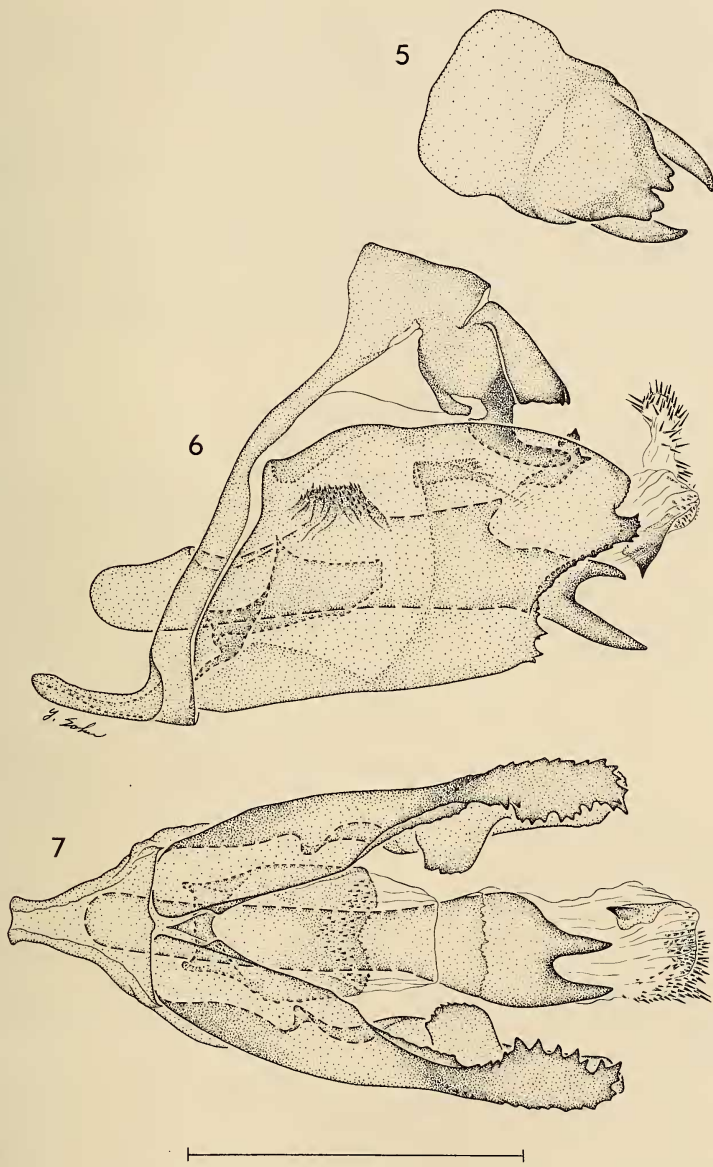
Two short prongs at distal end of aedeagus, one (lower) in the center and one (higher) on the right (Figs. 6, 7); central prong longer and directed noticeably downward (Fig. 6). Cornutal spines smaller and more numerous (Figs. 6, 7) than in *angellus*. The two discrete cornuti dissimilar: one with one or more short serrations sprouting from one end of a small, low base; the other with multiple serrations sprouting sharply along one side of a large, low base (Figs. 6, 7). As in *rica*, field of numerous tiny spines above aedeagus wider than long, and much wider than aedeagus (Figs. 6, 7).

Midventral, triangular projection of juxta large and more anteroventrally oriented than in *angellus* and *rica* (Figs. 6, 7).

Saccus the shortest in the genus (Figs. 6, 7).

Stigma (Fig. 12). Inconspicuous. Bipartite: a triangular element in the angle between the cubitus and vein 2, not quite filling the apex of that angle; plus a linear element immediately below, along the lower side of vein 2. All as in *angellus*.

Facies (Figs. 16, 17). Very like *angellus*. Forewing cell and dorsal hindwing without spots. Semihyaline spots of forewing dirty white to vaguely yellowish. That in space 2 somewhat suggestive of > on the left and < on the right, especially ventrally, but less



FIGS. 5-7. Male genitalia of *Halotus jonaveriorum*, holotype, from La Soledad-Buena Vista, Sierra Madre del Sur, 1525 m, Oaxaca, MEXICO, 12 April 1990, J. Kemner [X-2970] (USNM). Scale = 1.0 mm. 5, Tegumen, uncus, and gnathos in dorsal view; 6, Complete genitalia (minus right valva) in left lateral view, with vesica everted to show cornuti; 7, Valvae, aedeagus (vesica everted—the fancier of the two discrete cornuti does not show at this angle), juxta, field of spines above aedeagus, saccus, and ventralmost vinculum in ventral view.

than in *angellus* because the apex tends to fill in to make a triangular instead of angular spot. Of the three small subapical spots in spaces 6, 7, and 8, only 7 always developed. Small, linear, opaque yellow spot in space 1b dorsally, just above vein 1. Complex pattern of ventral hindwing mostly in shades of tan and brown and not contrasty.

Size (male forewing length). Mean 15.6 mm, range 14.5–17.2 mm, $n = 11$; the middle species.

Material examined. Holotype: MEXICO, OAXACA, Sierra Madre del Sur, La Soledad-Buena Vista, 1525 m, 12 April 1990, ♂, John Kemner [X-2970]; deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Paratypes: 10 ♂ taken by John Kemner at the type locality as follows: 12 April 1990, 1 ♂; 16 April 1990, 1 ♂; 6 May 1990, 2 ♂ [X-3243]; 21 November 1990, 4 ♂ [X-3078, X-3079, X-3244]; 2 December 1991, 2 ♂ (4 in the collection of H. A. Freeman, 6 in USNM).

Etymology. I am delighted to name this species for both John Kemner who collected all the material and H. Avery Freeman who spread it and passed it on. I have deliberately dropped the surname and “h” from each.

Halotus rica (Bell) (Figs. 8–10, 13, 18, 19)

Male genitalia (Figs. 8–10). Little or no gap between uncus and gnathos in lateral view (Fig. 9). Uncus comparatively narrow at its distal tip (Fig. 8). Each division of the very shallowly divided uncus (Fig. 8) dual in lateral view, with the subdivisions one above the other (Fig. 9) instead of side by side as in *angellus* and *jonaveriorum*.

In lateral view, rough point near middle of posterior margin of valva somewhat long and sharp; posterior margin above it more nearly straight and vertical (Fig. 9). “Bite” out of ventrolateral corner of valva comparatively shallow and straight edged (Fig. 9). Inwardly produced, wickedly dentate, “jawlike” flange set relatively low on valva—much closer to bottom than top of valva (Figs. 9, 10). Teeth on dorsal, oblong, anteromedially running projection of valva relatively coarse (Fig. 10).

Two short prongs at distal end of aedeagus, one (lower) on the left and one (higher) on the right (Figs. 9, 10); both (especially the right) curved gently downward (Fig. 9). Cornutal spines smaller and more numerous (Figs. 9, 10) than in *angellus*. The two discrete cornuti similar: each a single, sharp, conspicuous point sprouting from one end of a low, elongate base; base narrower in one cornutus than in the other (Figs. 9, 10). Field of numerous tiny spines above aedeagus wider than long, and much wider than aedeagus (Figs. 9, 10).

Midventral, triangular projection of juxta small (Figs. 9, 10).

Saccus intermediate in length (closer to *angellus*) (Figs. 9, 10).

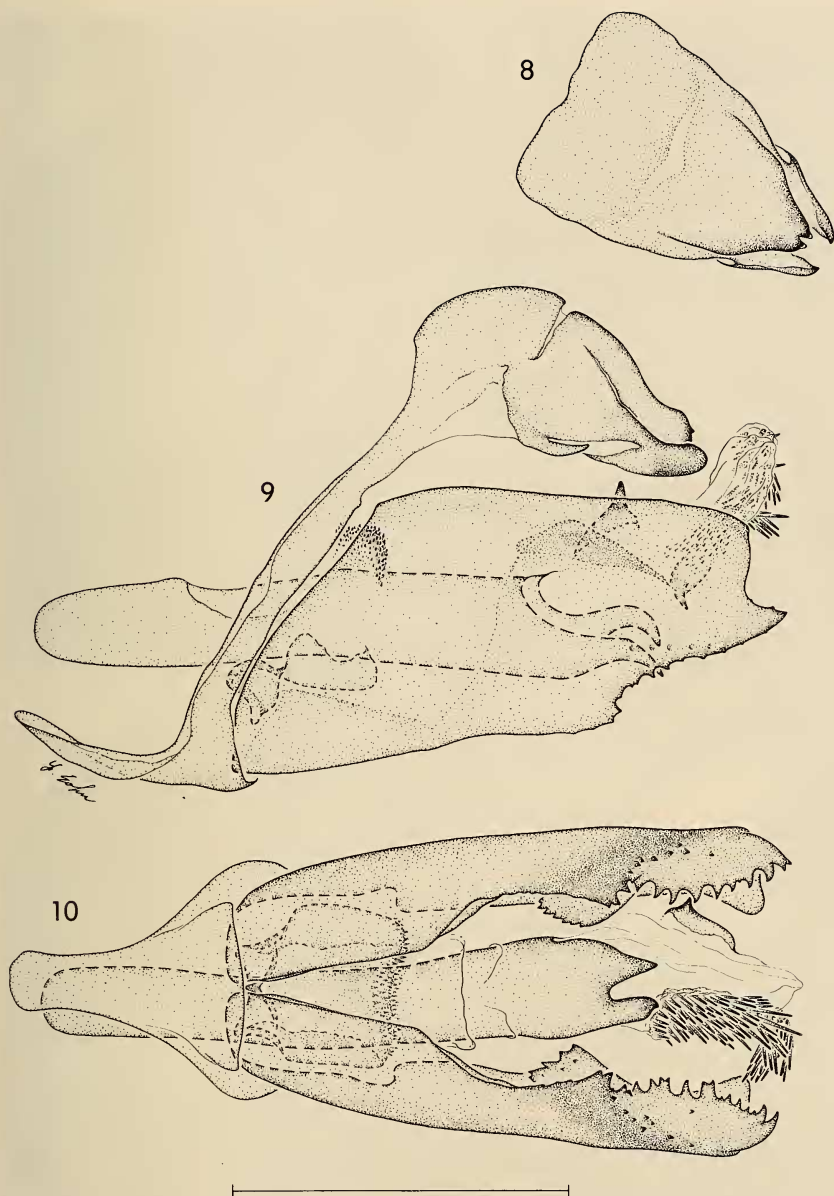
Stigma (Fig. 13). A little less inconspicuous than in *angellus* and *jonaveriorum*. Tripartite: a linear element running along the lower side of the cubitus from the origin of vein 3 to a point about half way toward the origin of vein 2, where it bends to cross space 2; a large spot immediately below, against the lower side of vein 2 in the top of space 1b; and a smaller spot just below that in about the middle of space 1b. Quite different from *angellus* and *jonaveriorum*.

Facies (Figs. 18, 19). Forewing cell with a dual semihyaline spot and dorsal hindwing with a total of five opaque yellowish orange spots—small and round in the cell but large and long in spaces 2, 3, 4, and 5 (the last two more or less fused). Semihyaline spots of forewing light yellowish orange. That in space 2 large and quadrate. Of the three subapical spots in spaces 6, 7, and 8, 6 and 7 always developed. Large, linear, opaque yellowish orange spot in space 1b dorsally, just above vein 1. Complex pattern of ventral hindwing mostly in shades of grayish white and brown and therefore contrasty. Relative to *angellus* and *jonaveriorum*, a well marked and jazzy skipper.

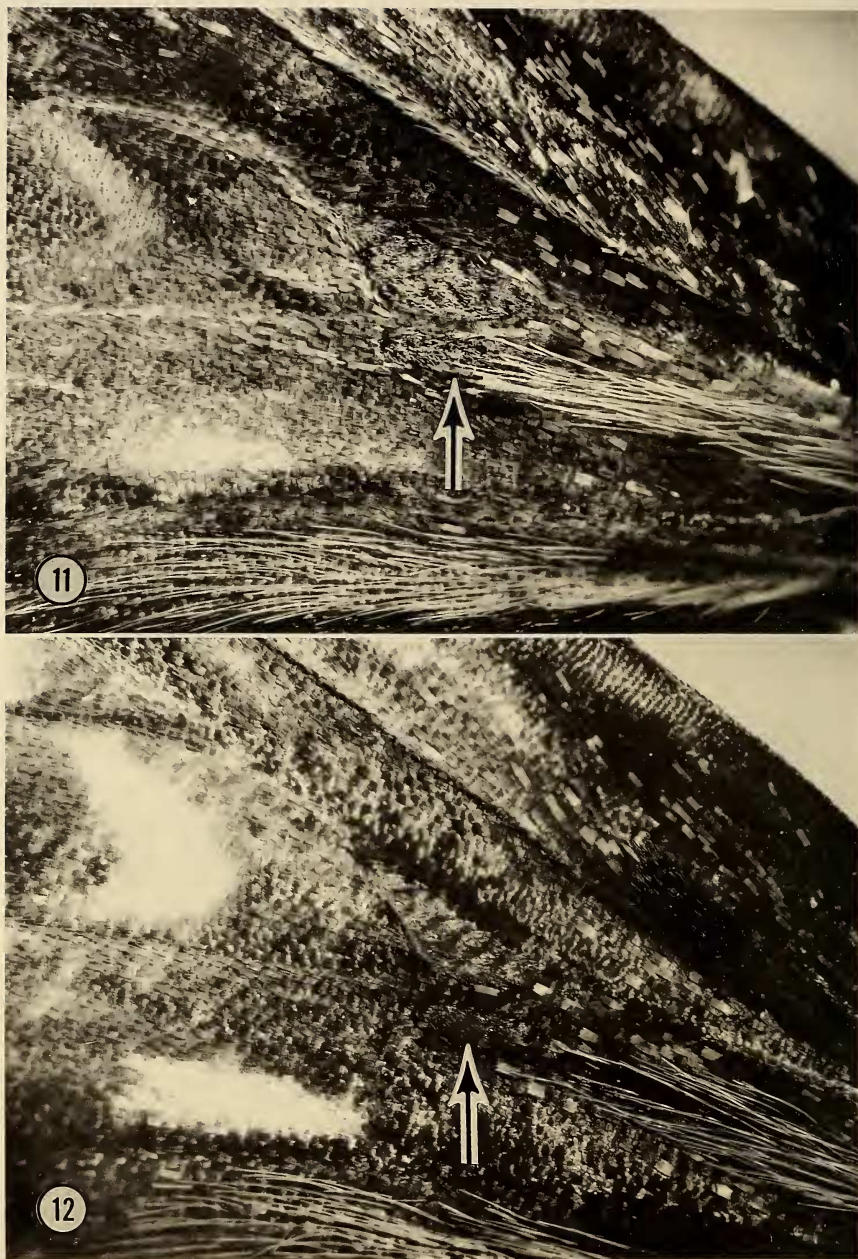
Size (male forewing length). Mean 17.1 mm, range 15.9–17.8 mm, $n = 4$; the largest species.

Type locality. Costa Rica.

Material examined. $n = 11$. MEXICO: JALISCO, Guadalajara, 1 ♂ [X-2332] (USNM). PUEBLA, Dos Caminos, 1220 m, July 1991, 1 ♂, M. Rangel [X-3245] (USNM). GUER-



FIGS. 8-10. Male genitalia of *Halotus rica* from El Zamorano, HONDURAS, 10 July 1980, R. D. Lehman [X-2404] (USNM). Scale = 1.0 mm. 8, Tegumen, uncus, and gnathos in dorsal view; 9, Complete genitalia (minus right valva) in left lateral view, with vesica everted to show cornuti; 10, Valvae, aedeagus (vesica everted—one of the two discrete cornuti does not show at this angle), juxta, field of spines above aedeagus, saccus, and ventralmost vinculum in ventral view.



FIGS. 11, 12. Bipartite male stigmata of *Halotus*: upper, triangular element is well to the right of the semihyaline angular to triangular spot in space 2 and lower, linear element (marked by arrow) is just across vein 2 in upper part of space 1b, well above and to the right of the opaque spot (in space 1b) which lies just above vein 1 of the left forewing. From specimens in Figs. 14-17. 11, *H. angellus*; 12, *H. jonaveriorum*, holotype.

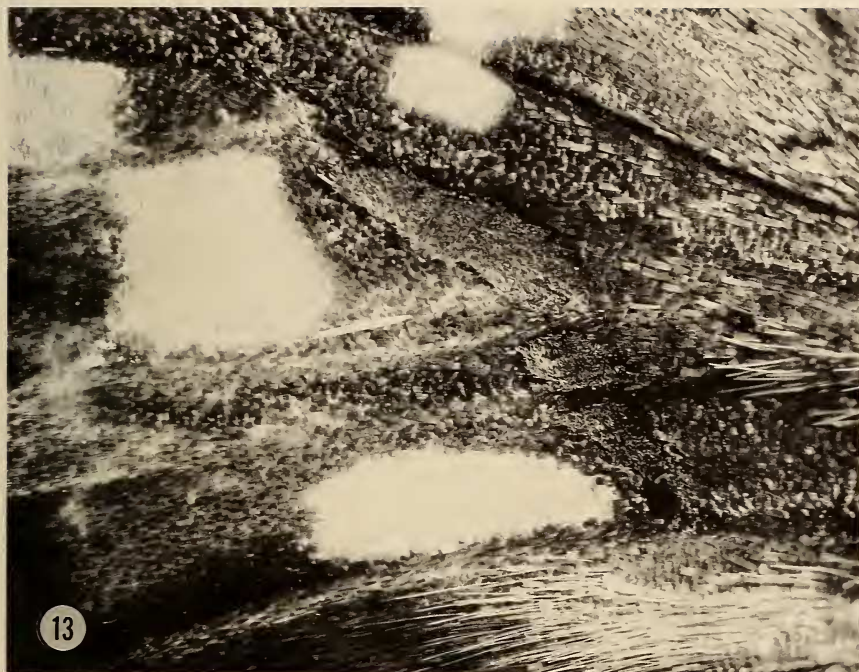


FIG. 13. Tripartite male stigma of *Halotus rica* extending from near the upper right corner of the quadrate semihyaline spot in space 2 almost to the right end of the opaque spot (in space 1b) which lies just above vein 1 of the left forewing. From specimen in Figs. 18, 19.

RERO, Acahuizotla, September 1960, 1 ♂, T. Escalante [H-660, H. A. Freeman] (AMNH). OAXACA, Oaxaca, 22 June 1966, 1 ♀, H. A. Freeman (AMNH). CHIAPAS: Muste, 24 August 1968 and 11 September 1968, 2 ♂, E. C. Welling (AMNH); San Jeronimo, vicinity Tacana Volcano, 450 m, 9 September 1970, 1 ♂, E. C. Welling (AMNH).

EL SALVADOR, Cojutepeque, 7 July 1952, 1 ♂ (USNM).

HONDURAS, El Zamorano, 10 July 1980, 1 ♂, R. D. Lehman [X-2404] (USNM).

COSTA RICA: 1 ♂ (holotype) [G 1130, E. L. Bell] (AMNH). San José, 13–18 November 1977, 1 ♀, W. H. Wagner [X-3246] (USNM).

Evans (1955:362) lists "1 ♀ Guatemala. 1 ♂ Ecuador (Zamora)" for *H. rica* in the collection of the British Museum (Natural History). Because the Ecuadorian male is the only specimen of *Halotus* I know of from south of Chiriquí, Panama, verification is desirable; but, because *Halotus* is still poorly represented in collections, the record may be real.

Reassociating *Halotus*

Evans (1955) makes *Halotus* the last genus in what is by far the largest division (the 22-genus *Hesperia* subgroup) of his 36-genus M or *Hesperia* group. In addition to *Hesperia*, this subgroup contains such familiar genera to American collectors as *Atalopedes*, *Polites*, *Wallengrenia*, *Atrytone*, *Poanes*, *Ochlodes*, and *Paratrytone*. I have been closely studying the genitalia of these skippers, particularly during the



FIGS. 14-19. Males of *Halotus* in dorsal (even numbered) and ventral (odd numbered) view (all $\times 1$). 14, 15, *H. angellus* from Volcán Baru, 1800 m, Chiriquí, PANAMA, 5 December 1976, S. S. Nicolay (USNM); 16, 17, *H. jonaveriorum*, holotype, from La Soledad-Buena Vista, Sierra Madre del Sur, 1525 m, Oaxaca, MEXICO, 12 April 1990, J. Kemner [X-2970] (USNM); 18, 19, *H. rica*, from El Zamorano, HONDURAS, 10 July 1980, R. D. Lehman [X-2404] (USNM).

past six years (Burns 1985, 1987, 1989, 1992, unpubl.), and see no special similarity between them and those of *Halotus*.

However, I do see similarities between the genitalia of *Halotus* (Figs. 1-10) and those of another neotropical genus, *Niconiades*, which is the last genus in the largest division (the 7-genus *Niconiades* subgroup) of Evans's (1955) 20-genus O or *Calpodus* group. Although the rough general resemblance, in itself, might not be significant, it is bolstered by specifics. *Niconiades*, like *Halotus*, produces a dentate, inwardly directed flange from the inner side of the distal part of the valva. In both genera, the aedeagus ends in one or two caudally directed, pointed prongs that range from short to long. Almost all species of *Niconiades* express the peculiar field of spines in membrane just above the aedeagus and well above the juxta (these crowded spines are larger in *Niconiades* than they are in *Halotus*). In my genitalic characterization of *Halotus*, the entire paragraph describing the juxta applies nearly as well to *Niconiades* (in *Niconiades*, the juxta is still more posterior than it is in *Halotus*, and the anterior margin of its transverse base is sometimes convex instead of concave).

I do not yet know enough about the genitalia of neotropical hesperiines across the board to say how close *Halotus* and *Niconiades* really

are. *Niconiades* differs strongly (and consistently) from *Halotus* in the form and also the length of the uncus (longer, instead of shorter, than the gnathos) and lacks cornuti, which are so characteristic in *Halotus*. A much larger genus, *Niconiades* varies much more in valval shape.

With respect to several classical nongenitalic characters, *Halotus* and *Niconiades* are not so different as wing shape and facies might at first suggest. (Facies is especially tricky to interpret since it shifts abruptly within each genus—in *Halotus*, compare *angellus* and *jonaveriorum* [Figs. 14–17] with *rica* [Figs. 18, 19]; *Niconiades* makes a bigger jump than that. Some *Niconiades*, like all *Halotus*, have checkered wing fringes.) Stigmas of *Niconiades* vary from bi- to tripartite (though not in the way that they do in *Halotus*). When bipartite, they usually resemble or exactly copy (in both form and position) the bipartite stigmas of *H. angellus* and *H. jonaveriorum* (Figs. 11, 12); and when tripartite, the upper two elements keep the bipartite positions on the wing. Antennae of *Halotus* are relatively longer, with less chunky clubs, than those of other *Hesperia* subgroup genera and hence are much like those of *Niconiades* (the nudum is shorter in *Halotus* [11 to 13 segments, distributed 3/8 to 4/9] than it is in *Niconiades* [13 to 16 segments, distributed 5/8 to 7/9]). Palpi are remarkably similar in *Halotus* and *Niconiades*.

Because these—and other (Burns 1990)—related genera are far apart in Evans's (1955) system, it is fatally flawed. In that connection, it is abundantly and painfully clear to me that *Niconiades* is nowhere near other genera in Evans's *Niconiades* subgroup such as *Thespies*, *Vacerra*, and *Oxyntes*, and, furthermore, that *their* closest relatives are widely scattered in at least three major generic groups of Evans besides M and O—but that is another story.

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